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PROCEEDINGS
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FACET NUMBER AND THE v^+ HORMONE IN THE BAR EYE OF DROSOPHILA MELANOGASTER[1]

By Simon Chevais, Boris Ephrussi and Arthur G. Steinberg[2]

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Communicated August 4, 1938

Introduction.—Beadle and Ephrussi[3] and Steinberg and Abramowitz[9] have shown that eye discs of the Bar (*B*) "mutant" of *Drosophila melanogaster* when implanted, shortly before puparium formation, into vermilion (*v*) hosts are not autonomous with respect to pigmentation. It has been concluded therefore that the Bar eye normally receives some v^+ hormone[3,10] from the body and that, at the time of transplantation, it either had not received the substance or having received it was not able to use it. In both the above cited papers evidence was offered which indicated that the reduced ability of the *B* eye to form the v^+ hormone was not causally related to its smaller size. In other words the effect of the *B* "locus" on the facet number and on the pigment are believed to result from two separate reactions, both of which may, however, have had a common origin. If this hypothesis is correct it should be possible to affect the facet number without affecting the eye color and *vice versa*.

Ephrussi, Khouvine and Chevais[6] have shown that nitrogenous extracts of *Calliphora* larvae[7] which contain the v^+ hormone also have the ability to increase the facet number when supplied to *B* larvae by the feeding technique of Beadle and Law.[4] Provided the eye disc does not use the v^+ hormone prior to puparium formation (to be demonstrated below) the finding of Ephrussi, Khouvine and Chevais affords us a direct means of testing the above hypothesis.

Experiments and Discussion.—Two different experiments were performed to test the action of the *Calliphora* extracts on pigmentation before puparium formation: (*a*) *v B* larvae were raised on a medium consisting of a 2% agar solution containing 3% glucose and 11% of a nitrogenous extract of *Calliphora* larvae.[7] Shortly before pupation the eye discs of these larvae were implanted into *v* hosts raised on the standard food. After eclosion the flies were dissected and the implanted eyes compared with *v B*

eyes taken from larvae of the same age which had been raised on the standard food and which had also been implanted into *v* hosts; (*b*) the same experiment as above was performed with flies which were vermilion not-Bar. In the latter case both the test and control eyes were of the same size, while in the former the test eyes were larger than the controls. In neither case, however, was any difference observed between the pigmentation of the experimental and control eyes. It is evident therefore that the v^+ hormone supplied by the *Calliphora* extract does not produce a visible effect on the eye pigment under the conditions of the experiments reported in this paper. The method is therefore valid to test the independence of the ability to form the v^+ hormone from the facet number.

Approximately forty *B* and forty *v B* larvae, 40 hours after hatching, were placed in vials containing 3 cc. of the agar-extract medium (these larvae will be referred to hereafter as "treated larvae"). The 40-hour stage was chosen because the extract has its maximum effect when larvae are grown on the standard food up to this age and then transferred to the extract (Chevais, unpublished). All the other larvae involved in these experiments were raised on the standard food medium. For the transplantation mature larvae were used as both hosts and donors. The experiments were performed at 25 ± 0.2°C.

Eye discs from treated *B* males were implanted into *v* hosts. Males were used because the extract has a greater effect on them than on females.[5] As controls for the degree of pigmentation, discs from treated *B* and *v B* larvae were implanted into wild type and *v* hosts, respectively; in addition *B* discs from untreated larvae were implanted into *v* hosts in order to have a direct comparison between them and treated *B*. Finally, as still further controls for the pigmentation, *B* and *v B* eye discs from untreated larvae were implanted into wild type and *v* hosts, respectively. The facet numbers of the implants recovered from the experiments involving the implantation of treated *B* into *v* were determined and compared with those of *B* implants from untreated larvae (unfortunately, the sex of the donors was not determined in these controls and hence no real mean value can be given; in the *B* stock employed in this experiment the females have approximately 15 fewer facets than the males[5]). The facets of the male sibs of both the treated and untreated *B* larvae were also counted. The facet counts, summarized in table 1, show clearly that there has been a marked increase in the number of facets in both the implanted and unimplanted (*in situ*) eyes developing from the treated larvae as compared with the untreated controls. Moreover, the range as well as the mean of the facet number of the implanted eyes taken from treated males is the same as that of the untransplanted sib males. In general the same may be said for the untreated controls. We may conclude therefore that transplantation does not affect the facet number. This of course is not at all unexpected since at the time

when the discs were taken for transplantation the facet number is already determined.[8]

The comparison of the pigmentation showed that the *B* eyes from the treated larvae implanted into *v* hosts were slightly darker than the *v B* controls[9] (discs from treated *v B* larvae implanted into *v* hosts) and were identical in pigmentation with *B* eyes from untreated larvae which also had been implanted into *v* hosts.

The facet number of the treated *B* implants in *v* varies from 200 to more than 370 as shown in table 1; that is from the size of heterozygous double-infrabar ($B^iB^i/+$) to that of heterozygous Bar ($B/+$). Both $B^iB^i/+$ and $B/+$ when implanted into *v* hosts are very much darker than $v^{3,9}$; consequently there was a sufficient increase in facet number to enable us to detect a change in the degree of pigmentation if there was a direct correlation between facet number and the ability to form the v^+ hormone.

TABLE 1

FACET NUMBERS OF BAR EYES RECOVERED UNDER THE VARIOUS EXPERIMENTAL CONDITIONS LISTED IN THE FIRST COLUMN

	M	RANGE	N
Eyes from treated ♂♂ implanted into *v* hosts	256.5	200–370*	8
In situ eyes from treated ♂♂	241.8	210–285	16
Implanted eyes from untreated ♂♂ and ♀♀	65.1†	52–86	7
In situ eyes from untreated ♂♂	85.3	68–109	15

* The largest eye was partially destroyed during the dissection; the true number is therefore higher than 370.

† See text.

Since no change in the degree of pigmentation was observed, the data may be accepted as a further verification of the original conclusion of Beadle and Ephrussi that the decreased ability of the Bar eye to form the v^+ hormone is not due to its smaller size.

Summary.—Eye discs from Bar larvae, which had been fed a nitrogenous extract of *Calliphora* larvae, known to increase the facet number, were implanted into vermilion hosts.

Comparison with the proper controls showed that such increased Bar eyes (up to 370 facets) develop the same pigmentation as do eyes from Bar larvae raised on the standard food medium.

It is concluded that there is no direct correlation between facet number and the ability of the eye to form the v^+ hormone.

These results are in agreement with the similar conclusion previously drawn by Beadle and Ephrussi.

[1] Work done at the Institut de Biologie physico-chemique, Paris, France.

[2] Recipient of a grant from the Dykman Fund of the Department of Zoölogy of Columbia University.

[3] Beadle, G. W., and Ephrussi, Boris, *Genetics*, **21**, 225–247 (1936).

[4] Beadle, G. W., and Law, L. W., *Proc. Soc. Exptl. Biol. Med.*, **37**, 621 (1938).

[5] Chevais, Simon, and Steinberg, Arthur G. (in press).

[6] Khouvine, Yvonne, Ephrussi, Boris, and Chevais, Simon, *Nature*, **141**, 204–205 (1938).

[7] Khouvine, Yvonne, and Ephrussi, Boris, *C. R. Soc. Biol.*, **124**, 885 (1937).

[8] Medvedev, N. N., *Zt. Ind. Abstam. Vererbl.*, **70**, 55–72 (1935).

[9] Steinberg, Arthur G., and Abramowitz, Mortimer, *Proc. Nat. Acad. Sci.*, **24**, 107–111 (1938).

[10] The v^+ hormone—a substance necessary for the formation of the wild type eye pigmentation; when supplied to v flies this substance causes the eye color to approach that of wild type.

For the purposes of this experiment, v flies may be regarded as completely lacking the v^+ hormone.

AN X-RAY INDUCED INTERCALARY DUPLICATION IN DROSOPHILA INVOLVING UNION OF SISTER CHROMATIDS

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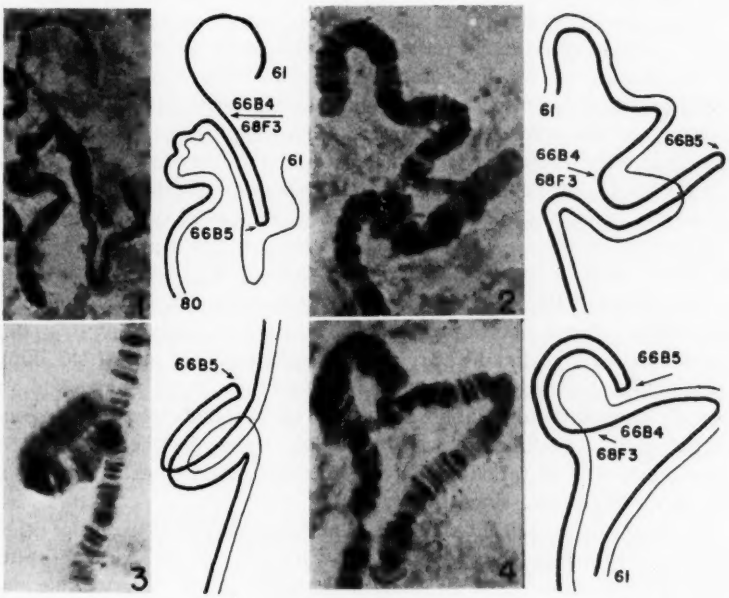
Communicated August 13, 1938

In a study recently completed in this laboratory, Carlson[1] has found striking evidence that sister chromatids of broken sections of irradiated neuroblast chromosomes of the Orthopteran, *Chortophaga*, may fuse *inter se* at the breakage points to produce either chromatid bridges, ring-shaped or V-shaped fragments, depending on whether they originally occupied proximal, intercalary or distal positions. Bauer, Demerec and Kaufmann[2] in appraising the evidence for and against the possible occurrence of single induced breaks have suggested that the rarity of unequivocal cases of terminal deficiencies and terminal inversions in Drosophila may be due to their elimination rather than to non-occurrence. Assuming that two chromatids of the same chromosome could unite at a breakage point, a bridge would be formed as the spindle attachment regions separate at anaphase. Rupture across the bridge with subsequent refusion of chromatids, and repetition of the process in successive mitoses would increase the genic unbalance in daughter nuclei so that non-viable combinations would result.

The present report is presented to show that two chromatids of a chromosome of *Drosophila melanogaster* with breaks at identical loci may unite with one another at these broken ends, and that under suitable conditions the resulting rearrangement may be perpetuated.

Salivary glands secured from an F_1 female larval descendant of a father irradiated at 3000 r-units showed a duplicated section of the left limb of the third chromosome extending from 66*B*5 to 68*F*3 of Bridges' 1935 map. The duplication is arranged in the pattern of a "reversed repeat," as may be represented by the sequence abcd*gfeef*ghijk. In several of the nuclei the two strands of paternal origin and the maternal chromosome had



FIGURES 1–4

Salivary gland chromosomes of intercalary duplication. In the diagrams shown to the right of each photograph the altered paternal strand is represented by the heavier line; the maternal, unaltered strand by the lighter line. The tip of 3*L* is marked by the figure 61; the spindle attachment end by the figure 80. Arrows indicate the inversion point and the limits of the duplicated section. Further description in the text.

conjugated to form a looped aggregate resembling the pairing configuration of an inversion heterozygote (figure 3). A striking feature of conjugation is the close association maintained between the duplicated regions of the 3*L* strand of paternal origin even when the maternal strand remains wholly or partially unpaired. As a result of this intimate lateral association the two linearly abutting homologous bands (the 66*B*5 bands) most frequently present the aspect of free ends of homologous strands (see figures 1, 2). A similar type of pairing of the duplicated intercalary sec-

tions inserted in the fourth chromosome in eyeless-dominant was observed by Bridges.[3]

Failure to observe evidence of linear continuity of the 66*B*5 bands suggested that we might possibly be dealing with a rearrangement involving translocation between the 66*B*5 ends and some poorly defined portion of the chromocentral region, such as those proximal chromomeres representing the short arms of the *X* and fourth chromosomes (Kaufmann[4]). Since the glands were obtained from an F_1 larva, it was impossible to secure additional salivary gland nuclei for study. Fortunately we had preserved the larval ganglia and were able to determine, as Bridges did in the case of eyeless-dominant, that the altered chromosome existed as a separate and continuous unit. Analysis of several mitotic figures of neuroblast and ganglion cells disclosed no perceptible alteration in the second, fourth or *X* chromosomes, although there was some intimation of difference in length between the two third chromosomes. We feel certain, therefore, that the sequence of banding in the altered third chromosomes is as follows:

61,62....66*B*4/68*F*3....66*B*5/66*B*5....68*F*3,69*A*1....80 sp. a. 81..100

The apparent lack of linear continuity across the 66*B*5/66*B*5 union in the salivary chromosomes presumably represents a rupture at this point due to the force of lateral attraction between identical loci of the duplicated regions, causing the chromosome to fold through 180 degrees. Lack of such intimate pairing in most of the reversed repeats which are present in nature in the chromosomes of Drosophila may be the result of the establishment of mutational differences between the duplicated sections in the period intervening since their origin.

It seems also significant that the duplicated sections of paternal origin are paired in practically every nucleus, whereas these two conjugate with the maternal strand in only some of the cells. Such observations suggest that when pairing is initiated, the proximity of adjacent bands favors their synapsis and the consequent conjugation of the duplicated sections prior to their union with the strand of maternal origin.

Whether the duplication results from strands which were split at the time of irradiation, or whether division and reunion occurred subsequently cannot be determined from this rearrangement. Data bearing on these problems have been obtained from other duplications and will be discussed in another publication.[5] In the present case we may assume that breaks occurred in 66*B* and in 68*F*, that at the time of reunion of the fragments the region between these points was present as twin strands, that the 68*F* end of one of the strands joined with the 66*B*4 end of the distal section of 3*L* to give an inverted section, and that the sister chromatids then fused at the 66*B*5 broken ends. The 68*F*3, 69*A*1 continuity may represent an unaltered sequence resulting from the fact that at the time of irradiation the chromosome had divided at this level and that only one

strand was broken, or the 68*F*3, 69*A*1 sequence may represent a refusion which would be necessary if both strands had broken at this level. The general plan of the rearrangement may be expressed as follows:

abcd|efg|hijk·lmnopqrstu
abcd|efghijk·lmnopqrstu giving abcd*gfeef*ghijk·lmnopqrstu

with probably another strand of the constitution: abcdhijk·lmnopqrstu. The fate of the latter chromosome remains conjectural, although it may as a result of the deficiency form a non-viable nucleus at the end of the first cleavage mitosis.

The union of sister chromatids of a chromosome in the manner here described offers a possible explanation of the origin in nature of the reversed repeats described by Bridges[6,7] and shown especially clearly in the 35*F*–36*D* regions of the left limb of the second chromosome. The same type of rearrangement has been postulated by Offerman[8] as an explanation of his interpretation of the structure of the bulb in division 2 of the *X* chromosome as a reversed repeat. If in such rearrangements the region of mirror-imaging is not too extensive to affect viability, and if it has selection value in nature, it may be expected to be perpetuated in phylogeny.

Summary.—An intercalary mirror-imaged duplication in the left limb of the third chromosome of *D. melanogaster* was found in an F_1 larval descendant of an irradiated father. Origin of the duplication is attributed to fusion at identical loci of the broken ends of two chromatids of the paternal third chromosome.

[1] Carlson, J. G., *Genetics* (in press).
[2] Bauer, H., Demerec, M., and Kaufmann, B. P., *Genetics* (in press).
[3] Bridges, C. B., *Trans. Dynamics of Develop.*, **10**, 463–474 (1935).
[4] Kaufmann, B. P., *Jour. Morph.*, **56**, 125–155 (1934).
[5] Kaufmann, B. P. (in preparation).
[6] Bridges, C. B., *Jour. Hered.*, **26**, 60–64 (1935).
[7] Bridges, C. B., *Ibid.*, **29**, 11–13 (1938).
[8] Offerman, C. A., *Jour. Genetics*, **32**, 103–116 (1936).

THE DISTRIBUTION OF GENE FREQUENCIES IN POPULATIONS OF POLYPLOIDS

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Communicated August 12, 1938

The theoretical distribution of gene frequencies in populations of diploid organisms, as affected by mutation, selection, migration and inbreeding, has been discussed in previous papers.[1,2] It is desirable to extend the theory to populations of polyploids.

Mutation and Migration.—Assume gene frequencies $[(1 - q)A + q\,a]$ where a is the gene under consideration and A represents its array of alleles (without any implications with respect to dominance). Zygotic frequencies rapidly approach an equilibrium under random mating, the equilibrium distribution in $2k$-ploids being the expansion of $[(1 - q)\,A + q\,a]^{2k}$ (Haldane[3]).

Mutation pressure is the same as with diploids. Letting u be the rate of mutation from a, and v the rate of mutation to a, the rate of change of gene frequency per generation is

$$\Delta q = v(1 - q) - uq. \tag{1}$$

Crossbreeding pressure also is the same as with diploids. Letting q_t be the gene frequency of the species as a whole and m the effective amount of exchange between the local population in question and the species as a whole we have:

$$\Delta q = -m(q - q_t). \tag{2}$$

Any results for mutation pressure can be transformed into ones for crossbreeding pressure by substituting $m(1 - q_t)$ for u and mq_t for v. For simplicity, we will develop conclusions for mutation pressure only.

Selection Pressure.—The simplest kind of selection is that in which the selective values (W) of the various zygotes deviate from standard in proportion to the number of replacements of type genes (the case of no dominance).

ZYGOTE	FREQUENCY	W
A^{2k}	$(1 - q)^{2k}$	1
$A^{2k-1}a$	$2kq(1 - q)^{2k-1}$	$1 - s$
.....	.....	.....
a^{2k}	q^{2k}	$1 - 2ks$

$$\overline{W} = 1 - 2ksq. \tag{3}$$

$$\Delta q = -\frac{sq(1-q)}{1-2ksq} = \frac{q(1-q)d\overline{W}}{2k\overline{W}\,dq}. \tag{4}$$

In the more general case in which $\overline{W}$ is not related linearly to q because of more or less dominance, the momentary selective advantage of replacing A by a is still $\frac{d\overline{W}}{dq}$ and the formula for Δq is still given by (4).

Still more generally, if there is interaction between different series of alleles, and a selective value, W, is assigned each combination, the rate of change of the frequency of a particular gene under selection (with specified values of all other gene frequencies) is given by the formula

$$\Delta q = -\frac{q(1-q)}{2k\overline{W}}\frac{\partial \overline{W}}{\partial q}. \tag{5}$$

Inbreeding.—The effect of restriction in the effective size of population can be worked out by means of path coefficients.[1,4,5] In a $2k$-ploid the zygote may be considered as equally and completely determined by the $2k$ component genes.

Let y be the path coefficient measuring the contribution of gene to zygote and let f be the correlation between genes due to inbreeding. Expressing the complete determination of zygote by genes in an equation:

$$2ky[y + (2k-1)yf] = 1.$$

$$y^2 = \frac{1}{2k[1+(2k-1)f]}. \tag{6}$$

The path coefficient (x) expressing the contribution of the zygote to a single gene of a gamete must equal the correlation coefficient as there is only one connecting path.

$$x = y + (2k-1)yf$$

$$x^2 = \frac{1+(2k-1)f}{2k}. \tag{7}$$

$$xy = \frac{1}{2k}. \tag{8}$$

The zygote may also be considered as equally and completely determined by the two uniting gametes and each of these by its component genes. From this point of view, there are two kinds of correlation between component genes: between genes of the same gamete (c) and between genes of different gametes (d). The average correlation (f) is thus:

$$f = \frac{(k-1)c + kd}{2k-1}. \tag{9}$$

Under the simplest theory of segregation in polyploids (Muller[6]) the correlation between genes of the same gamete must be the same as between two *different* genes of the parental zygote. Using primes to designate preceding generations

$$c = f'. \tag{10}$$

There is a possibility (greatest for loci remote from the spindle fibre) that a gamete in a polyploid may contain more than one representative of the same parental gene (Haldane[3]) but the possible modification of the results due to this complication cannot be great and will not be considered here.

The correlation between genes of uniting gametes can be obtained by tracing the connecting paths according to the system of mating.

The proportion of unlike pairs of genes among pairs drawn from zygotes will be represented by p. In diploids this is the percentage of heterozygosis.[1] The relation of p to f is easily found by constructing the correlation table for f. For the present purpose two A's are considered like genes (two non-a's) even though they may actually be different alleles of a.

	A	a	
a	$p/2$	$q - p/2$	q
A	$1 - q - p/2$	$p/2$	$1 - q$
	$1 - q$	q	1

$$f = 1 - \frac{p}{2q(1-q)}. \tag{11}$$

Self-Fertilization.—In this case $d = x'^2$. From this result and (9), (10) and (7)

$$f = \frac{1 + (4k-3)f'}{2(2k-1)}. \tag{12}$$

$$p = \left[\frac{4k-3}{4k-2}\right] p'. \tag{13}$$

Following are special cases:

Diploid	$p = {}^1/_2 p'$	Hexaploid	$p = {}^9/_{10} p'$
Tetraploid	$p = {}^5/_6 p'$	Octoploid	$p = {}^{13}/_{14} p'$

Haldane[3] has studied the effects of self-fertilization by a direct consideration of all types of zygotes. He represents the symmetrical case in tetraploids as $p_n A^4 : q_n A^3 a : r_n A^2 a^2 : q_n A a^3 : p_n a^4$ where $2p_n + 2q_n + r_n = 1$. $p_1 = q_1 = 0, r_1 = 1$.

He shows that the following relations hold

$$p_{n+1} = p_n + {}^1/_4 q_n + {}^1/_{36} r_n$$
$$q_{n+1} = {}^1/_2 q_n + {}^2/_9 r_n$$
$$r_{n+1} = {}^1/_2 q_n + {}^1/_2 r_n.$$

The proportion of unlike pairs of genes in zygotes (p of the present paper) is $q + ({}^2/_3)r$. It may easily be seen that $(q_{n+1} + {}^2/_3 r_{n+1}) = {}^5/_6(q_n + {}^2/_3 r_n)$ or $p = {}^5/_6 p'$ in our terminology.

Haldane has similarly derived the consequences of self-fertilization in hexaploids. Our formula, $p = {}^9/_{10} p'$ is in agreement.

GROUPS OF N MONOECIOUS INDIVIDUALS

Random Self-Fertilization.—Extension can easily be made to larger inbreeding groups. In the case of N monoecious individuals with self-fertilization at random the chance of selfing is $\frac{1}{N}$ and of union of gametes from different individuals is $\frac{N-1}{N}$. Giving due weight to these two possibilities

$$d = \frac{1}{N} x'^2 + \frac{N-1}{N} (4k^2 x'^2 y'^2) d' \qquad (14)$$
$$= \frac{1}{2Nk} [1 + (2N-1)(2k-1)f' - (2N-2)(k-1)f'']$$

$$p = \frac{1}{2N(2k-1)} [(6Nk - 4N - 2k + 1)p' - (2N-2)(k-1)p'']. \qquad (15)$$

This reduces to $p = \left(\frac{4k-3}{4k-2}\right)p'$ if $N = 1$ (self-fertilization) but if N is large it is approximately $p = \left(1 - \frac{1}{2Nk}\right)p'$.

No Self-Fertilization.—With N monoecious individuals and self-fertilization excluded, the chance of matings between siblings is $\frac{2}{N(N-1)}$, between half-siblings is $\frac{4(N-2)}{4(N-1)}$ and of more remote matings $\frac{(N-2)(N-3)}{N(N-1)}$.

Using these weights:

$$d = \frac{1}{N(N-1)} (x'^2 + d') + \frac{N-2}{N(N-1)} (x'^2 + 3d') + \frac{(N-2)(N-3)}{N(N-1)} d'. \qquad (16)$$

$$p = \frac{1}{2N(2k-1)}\left[(6Nk - 4N - 4k + 2)p' - (2Nk - 2N - 4k + 3)p''\right]. \quad (17)$$

This also reduces approximately to $p = \left(1 - \frac{1}{2Nk}\right)p'$ if N is large.

Mating of Siblings.—If $N = 2$ in the preceding case (mating of siblings)

$$p = p' - \frac{1}{8k-4}(2p' - p''). \quad (18)$$

With constant size of population it is legitimate to put $p/p' = p'/p''$ to find the limiting relation between successive generations.

$$p = \left[\frac{4k - 3 + \sqrt{16k^2 - 16k + 5}}{8k - 4}\right]p' \text{ approximately.} \quad (19)$$

Following are special cases:

	EXACT	LIMITING
Diploid	$p = p'/2 + p''/4$	$p = 1/4(1 + \sqrt{5})p' = 0.80902p'$
Tetraploid	$p = 5/6p' + p''/12$	$p = 1/12(5 + \sqrt{37})p' = 0.92356p'$
Hexaploid	$p = 9/10p' + p''/20$	$p = 1/20(9 + \sqrt{101})p' = 0.95249p'$
Octoploid	$p = 13/14p' + p'/28$	$p = 1/28(13 + \sqrt{197})p' = 0.96556p'$

Bartlett and Haldane[7] gave the limiting result in tetraploids in a form equivalent to $p = 0.92356p'$, from the pertinent solution of an octic equation derived from the iteration equations for all possible types of mating. This agrees with our result.

Sampling Variance.—In a population of N $2k$-ploids with gene frequencies $[(1 - q)A + qa]$ and *random* association of genes in the gametes (i.e., $p = 2q(1 - q)$) the variance of q among progeny populations, resulting from random samples of $2N$ gametes is

$$\sigma^2_{\Delta q} = \frac{q(1-q)}{2Nk}. \quad (20)$$

Unfortunately the association of genes in gametes is not wholly a random one. For example, a tetraploid $AAaa$ produces gametes in the proportions $1/6\,AA : 4/6\,Aa : 1/6\,aa$ (if A is near the spindle fibre) while under random association the proportions would be $1/4\,AA + 2/4\,Aa + 1/4aa$. However, the departure from (20) is slight except in very small populations. In the extreme case of self-fertilization ($N = 1$) it may easily be shown that $\sigma^2_{\Delta q} = \frac{q(1-q)}{4k-2}$.

The Distribution of Gene Frequencies.—A formula for the distribution of gene frequencies in populations subject to evolutionary pressure Δq and sampling variance $\sigma^2_{\Delta q}$ was reached in a previous paper.[8]

$$\varphi(q) = (C/\sigma^2_{\Delta q})e^{2\int(\Delta q/\sigma^2_{\Delta q})dq} . \qquad (21)$$

The approximate formula for the distribution of q in $2k$-ploids is thus as follows, letting $\Delta q = v(1-q) - uq + \frac{q(1-q)}{2k\overline{W}}\frac{d\overline{W}}{\partial q}$ from combination of (1) and (4) and letting $\sigma^2_{\Delta q} = q(1-q)/2Nk$.

$$\varphi(q) = C\overline{W}^{2n} q^{4nkv-1}(1-q)^{4nku-1}. \qquad (22)$$

The joint distribution for a system of multiple genes can be written as follows, letting $\overline{W}$ here be the mean selective value of the population in terms of all gene frequencies as variables.

$$\varphi(q_1 \ldots q_n) = C\overline{W}^{2n}\Pi[q_i^{4nk_iv_i-1}(1-q_i)^{4nk_iu_i-1}]. \qquad (23)$$

It is to be noted that this applies to aneuploids (k variable) as well as to euploids (k constant).

[1] Wright S., *Genetics*, **6**, 111–178 (1921).
[2] Wright S., *Proc. Nat. Acad. Sci.*, **23**, 307–320 (1937).
[3] Haldane, J. B. S., *Jour. Genetics*, **22**, 359–372 (1930).
[4] Wright, S., *Proc. Nat. Acad. Sci.*, **19**, 411–420 (1933).
[5] Wright, S., *Ann. Math. Stat.*, **5**, 161–215 (1934).
[6] Muller, H. J., *Amer. Nat.*, **48**, 508–512 (1914).
[7] Bartlett, M. S., and J. B. S. Haldane, *Jour. Gen.*, **29**, 175–180 (1934).
[8] Wright, S., *Proc. Nat. Acad. Sci.*, **24**, 253–259 (1938).

THE MECHANISM OF DELAYED KILLING OF MAIZE SEEDS WITH X-RADIATION

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Biological response to x-rays has often been interpreted on the basis of the quantum theory of radiation absorption and the so-called hit theory[1] involving the concept of a particular sensitive volume within the material. For the death of single-celled individuals it is frequently found that survival-dosage curves show a simple exponential relationship indicating the presence of one sensitive volume which requires only one hit or penetration by an electron in order to produce death. When multi-cellular systems

are studied it is usually found that the survival curves are no longer exponential but have a sigmoid shape. The hit theory in this case has two indistinguishable alternatives; either death occurs from a number of hits within one sensitive volume or a different number of hits within two or more sensitive volumes.

Certain tests of this theory will be described for the x-ray treatment of corn seeds. In this instance the seed embryos under investigation are large enough for scanning experiments designed for the purpose of searching for the position of a possible single sensitive volume. Killing in this case comes at a particular stage in the growth of the seedlings as a result of irradiation of the dry seeds with dosages ranging from 50,000 to 100,000 "r" units. Within approximately one week after the emergence of the plumule elongation ceases and usually a thick crumpled first leaf will show. After elongation has stopped the seedling remains green for about another week before dying. The maximum height obtained is about 1 to 2 cm. This type of death has been called delayed killing[2] and figure 1 illustrates the manner in which it occurs. A continuous band of radiation is used with a maximum intensity at 0.50 Å and a short wave-length limit of 0.26 Å. Dosage values are given to within 5 per cent as determined by an open air ionization chamber.[3]

Experimental survival ratio-dosage relationships are shown in figure 2 where a sigmoid-shaped curve is obtained. Interpretation of these results can be made from a consideration of the hit theory which is formulated in the following manner:[1] Given Z_0 seeds each with one sensitive volume v(cm.^{3}) which requires n successive hits or penetrations by primary electrons in order to produce delayed killing, then the number Z which survive a dosage of q ("r" units) will be given by the following Poisson series:

$$\frac{Z}{Z_0} = e^{-\alpha q}\left(1 + \alpha q + \frac{(\alpha q)^2}{2!} + \frac{(\alpha q)^3}{3!} + \ldots + \frac{(\alpha q)^{n-1}}{(n-1)!}\right) \quad (1)$$

where α represents the number of times the sensitive volume v is hit by primary electrons per "r" unit measured. It has been shown by Glocker[1] that when the range of the primary electrons is taken into account

$$\alpha = N_0 \cdot \frac{R + a}{a} \cdot v \quad (2)$$

N_0 being the number of primary electrons formed per cm.^{3} per "r" unit measured, R the range of the primary electrons in the biological material and a the average path traversed by the primary electrons in a spherical sensitive volume of radius r when $R >> a$, thus $a = \frac{4}{3}$r. Equation 1 can be evaluated by means of the incomplete gamma-functions from tables

prepared by Karl Pearson. A theoretical survival curve which approximately fits the experimental curve is shown in figure 2. In this case α

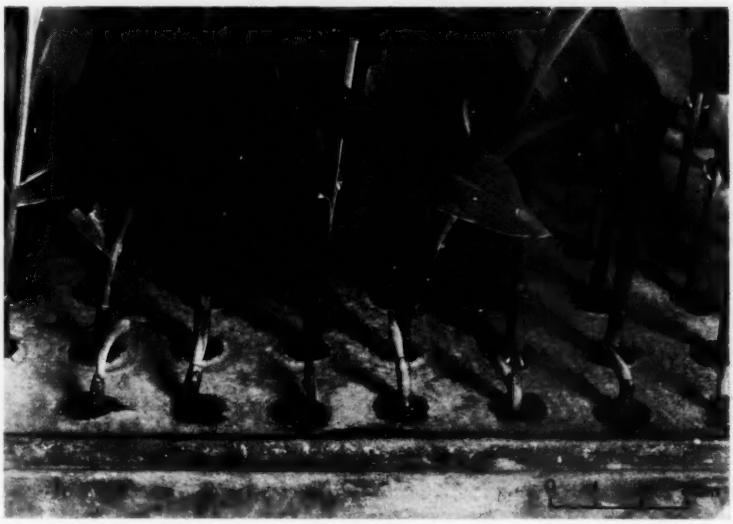

FIGURE 1

Photograph of delayed killed corn plants shown in the first row as compared with normal seedlings.

was taken equal to 4.5×10^{-4} ("r" units)$^{-1}$ which established the relationship between α and q. A value of $n = 14$ was obtained by selecting

TABLE 1

SUMMARY OF RESULTS OBTAINED WITH $^1/_2$ MM. SLIT WIDTH

ZONE NUMBER IRRADIATED	DOSAGE "r" UNITS	NUMBER OF SEEDS GERMINATED	PERCENTAGE SHOWING DELAYED KILLING	MEAN HEIGHT OF DEAD PLANTS (CM.)
6	50,000	83	none	.....
7	50,000	45	none	.....
8	50,000	125	none	.....
9	50,000	42	none	.....
10	50,000	274	none	.....
11	50,000	42	none	.....
12	50,000	123	none	.....
13	50,000	42	none	.....
14	50,000	122	none	.....
16	50,000	81	none	.....
10	100,000	60	none	.....
10	300,000	248	43.0	6.6 ± 0.8*

* Standard error of mean

the proper slope for the theoretical curve. The spherical sensitive volume required by equation 2 is approximately 1×10^{-15} cm.^{3} assuming the primary electrons to be the effective particles. This calculation was made on the basis of monochromatic radiation of wave-length 0.50 Å which is close to the average wave-length used.

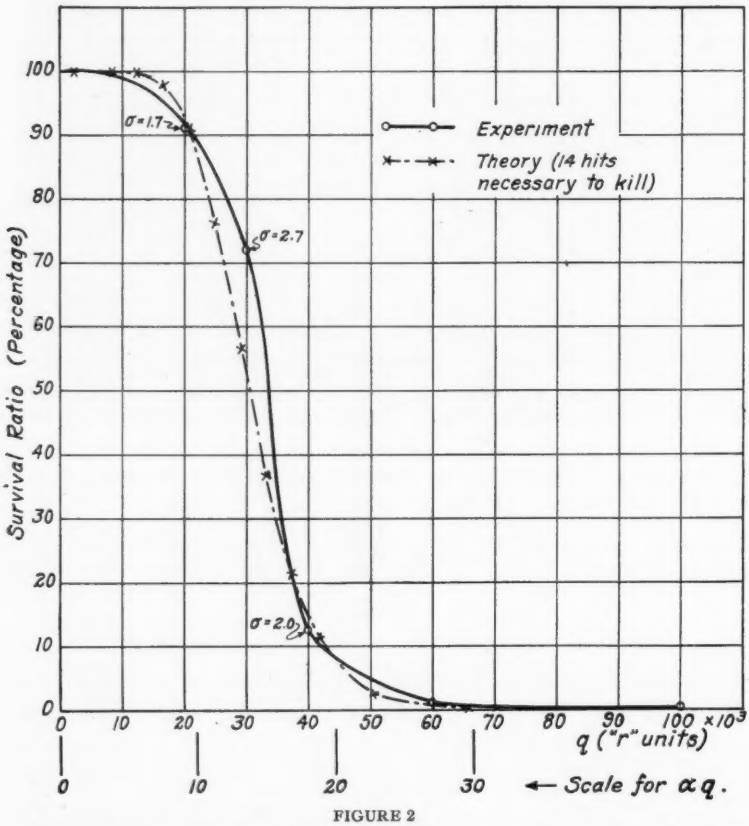

FIGURE 2

Survival ratio curves for the delayed killing of corn seeds. Values for the standard deviation (σ) are given for the experimental points.

A search for this sensitive volume was made by irradiating various assigned zones laid out crosswise of the seed as indicated in figure 3, while figure 4 shows the seed rack with lead slits used for the scanning experiments. Photographic films placed in the position occupied by the seed embryos provided a test for the actual width of the irradiated area ob-

tained. In table 1 are given the results of treatment taken over the length of the embryos with an irradiation area $^1/_2$ mm. in width. On the basis of a single sensitive volume contained within the embryo (which is about 7 mm. long) it is expected on the average that at least one out of every fourteen seeds or not less than 7% of the seeds should be killed. However, it is seen from table 1 that no delayed killing is observed for dosages of 100,000 "r" units or less involving treatment of more than 1000 seeds. The probability that this failure to kill could be the result of random sampling is so remote as to *eliminate the possibility of the existence of a single "sensitive volume" as defined by the hit theory.* At 300,000 "r" units a large

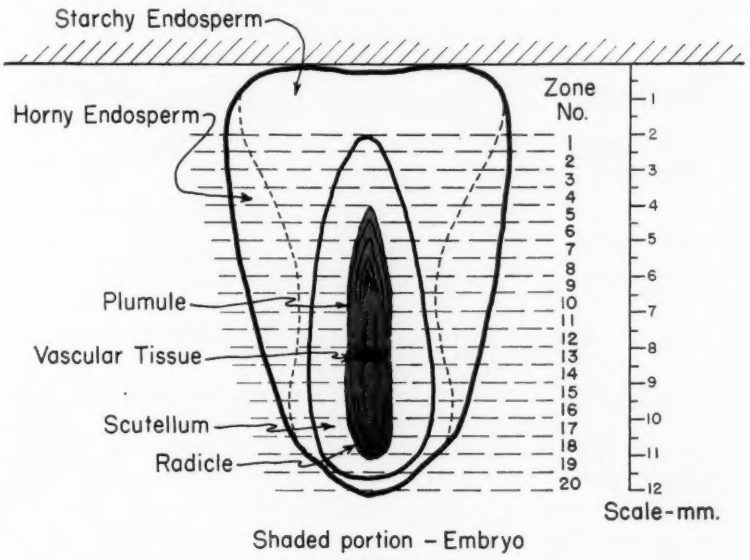

FIGURE 3

Drawing of a typical corn seed showing various zones used for irradiation.

number of the plants were killed but at a later stage in growth, indicating a different type of response.

Table 2 shows the results obtained for various wider slit widths and for exposures taken through the central portion of the seed embryos. It is seen that death occurs at the lower dosages and that, in general, a larger percentage of deaths will take place as the slit width is increased. However, in no case does complete killing exist even at the higher dosages. *The percentage death approaches a saturation value thus indicating that it is not proportional to the total amount of energy absorbed in a restricted region of the seed.* From table 2 it is also noticed that the plants die at earlier

stages as the slit width is increased, approaching for a 3 mm. slit width the average height of 1 to 2 cm. found for delayed death when the entire seed is exposed.

TABLE 2

SUMMARY OF RESULTS OBTAINED WITH 1.0 MM., 1.5 MM., 2.0 MM. AND 3.0 MM. SLIT WIDTHS

SLIT WIDTH	ZONE NUMBER IRRADIATED	DOSAGE "r" UNITS	NUMBER OF SEEDS GERMINATED	PERCENTAGE SHOWING DELAYED KILLING	MEAN HEIGHT OF DEAD PLANTS (CM.)
1.0 mm.	9, 10	20,000	44	36.4	2.1
	9, 10	29,200	176	16.9	.....
	9, 10	30,000	45	48.9	6.6
	9, 10	40,000	44	52.3	7.5
	9, 10	50,000	393	33.6	.....
	9, 10	52,000	134	30.5	.....
	9, 10	60,000	45	48.9	9.8
	9, 10	70,000	247	47.0	6.8
	9, 10	80,000	43	51.2	6.8
	9, 10	90,000	44	50.0	7.0
	9, 10	95,000	88	63.6	4.4
	9, 10	100,000	332	38.6	6.0
	9, 10	150,000	112	36.6	4.8
1.5 mm.	LH* 9, 10, 11, UH 12	31,600	177	10.7	.....
	8, 9, 10	40,000	34	2.9	1.2
	LH 9, 10, 11, UH 12	43,500	32	69.0	3.8 ± 0.9
	LH 9, 10, 11, UH 12	54,500	129	44.4	.....
	8, 9, 10	80,000	71	49.5	3.4
	8, 9, 10	120,000	65	57.0	2.2
	8, 9, 10	160,000	36	50.0	1.2 ± 0.5
	LH 9, 10, 11, UH 12	200,000	21	67.0	0.8 ± 0.9
	LH 9, 10, 11, UH 12	300,000	18	56.0	3.0 ± 1.2
2.0 mm.	9, 10, 11, 12	100,000	79	64.1	3.3 ± 0.75
3.0 mm.	8, 9, 10, 11, 12, 13	20,000	36	none	.....
	8, 9, 10, 11, 12, 13	33,200	178	23.6	.....
	8, 9, 10, 11, 12, 13	40,000	69	50	2.2
	8, 9, 10, 11, 12, 13	58,000	132	70	.....
	8, 9, 10, 11, 12, 13	60,000	69	72	1.7 ± 0.28
	8, 9, 10, 11, 12, 13	100,000	33	87	1.4
	8, 9, 10, 11, 12, 13	150,000	30	87	2.0
	8, 9, 10, 11, 12, 13	300,000	21	95	1.6

* LH means lower half. UH means upper half.
Variations given represent standard error of mean.

Probing experiments taken over the entire length of the seed with a 2 mm. slit width are summarized in table 3. It is seen that there is a wide distribution of positions on the seed in which death occurs, with the most sensitive region located at the approximate center of the embryo. One

hundred seeds were dissected and measurements taken of the variation in position of the seed embryos. It was found that the position of the center of the embryo will have a standard deviation of approximately 0.5 mm. This fluctuation may account in part for the wide distribution of susceptible volumes. However, these sensitive volumes are many magnitudes larger than expected on the pure formal hit theory as described above.

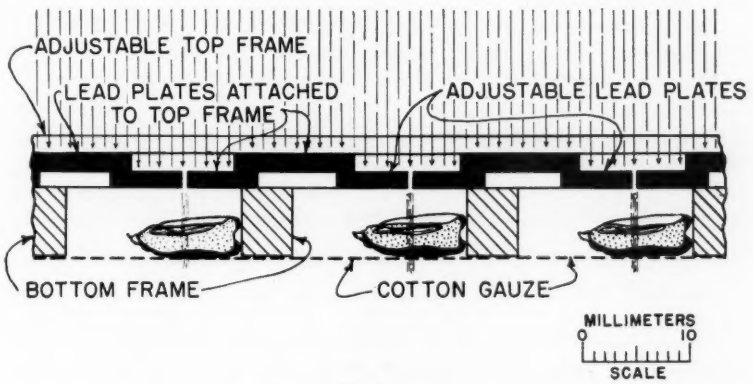

FIGURE 4

Diagram of lead slit arrangement used for irradiation.

For a multi-cellular organism such as a corn seed it is possibly not surprising that the hit theory interpretation based on the response of a single sensitive volume should fail. The alternative explanation involving a distribution of several sensitive volumes each requiring a certain number of

TABLE 3

RESULTS OBTAINED FROM SCANNING WITH 2.0 MM. SLIT WIDTH

ZONE NUMBER IRRADIATED	DOSAGE "r" UNITS	NUMBER OF SEEDS GERMINATED	PERCENTAGE SHOWING DELAYED KILLING	MEAN HEIGHT OF DEAD PLANTS (CM.)
1, 2, 3, 4	100,000	78	1.3	9.5
5, 6, 7, 8	100,000	82	32.1	2.1 ± 0.35
9, 10, 11, 12	100,000	79	64.1	3.35 ± 0.75
13, 14, 15, 16	100,000	81	11.1	6.51 ± 1.10
17, 18, 19, 20	100,000	76	0.0	.....

Variations given represent standard error of mean.

hits is not eliminated. However, on the basis of the above experiments it is safe to conclude that if multiple sensitive volumes do exist they are not contained within a spherical volume whose diameter is less than 0.5 mm.

The writer is indebted to Mr. G. N. Collins and Mr. J. H. Kempton, Bureau of Plant Industry, U. S. Department of Agriculture, for their helpful coöperation. They have made this work possible by taking charge of the planting and the collection of the data used on the growth of the plants.

[1] See for instance Glocker, R., *Zeit. Phys.*, **77**, 653–675 (1932).

[2] Collins, G. N., and Maxwell, L. R., *Science*, **83**, 375–376 (1936); Maxwell, L. R., *Phys. Rev.*, **51**, 375 (1937).

[3] For the design used see Taylor, L. S., and Singer, G., *Radiology*, **15**, 637–646 (1930).

CONTACT EFFECTS BETWEEN PLANT ROOTS AND SOIL COLLOIDS

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Introduction.—The prevailing theories of mineral absorption by plants from soils are based on the concept of the *soil solution*. They postulate that a nutrient element must be an integral part of the soil solution before it can be taken up by plant roots. An ion is said to be in the soil solution when it is detached from the solid phase and can diffuse freely. It closely follows the movements of the liquid phase. Essentially, the soil solution is identified with the nutrient solution of the plant physiologist.

Equation (1) schematically illustrates the action of plant roots in soils as visualized by the soil solution theory.

$$\boxed{\text{Root}} \longrightarrow \underbrace{m\,(H_2CO_3)}_{\text{In soil solution}} + \boxed{\begin{matrix}\text{Clay}\\ K\end{matrix}} \longrightarrow \boxed{\begin{matrix}\text{Clay}\\ H\end{matrix}}^{K} + \underbrace{K(HCO_3) + (m-1)(H_2CO_3)}_{\text{In soil solution}} \qquad (1)$$

The roots excrete carbonic acid into the liquid phase surrounding the soil particles. The H ions replace K from the surface of soil colloids and the resulting potassium bicarbonate is now ready for intake by roots.

In this paper an additional mechanism of mineral intake by plants from soils is proposed. It is based on the phenomenon of ion interchange existing between two surfaces which are in contact.

Theory of Contact Exchange.—Colloidal clays are negatively charged and possess high capacities for cation adsorption. The cations on the surface of the colloidal particles are not held rigidly. As a result of thermal agitation the ions oscillate and, at times, may be at considerable distances from the surface; but they remain in the field of force emanating from the colloid. Although the ions are surrounded by water molecules, they are not in solution in the sense that they can diffuse freely. The cations are under conditions of constraint and follow closely the movements of the colloidal particle to which they are attached.

These surface cations may be freed by exchange and then become an integral part of the intermicellar liquid or soil solution. According to the kinetic theory of ionic exchange[1] release may occur when a replacing ion enters the oscillation space of the adsorbed cation, as illustrated in figure 1. This process forms the basis for the mechanism represented by equation (1).

Conceivably, ionic exchange might also occur if two oscillation spaces overlap. This process may take place between neighboring ions on the

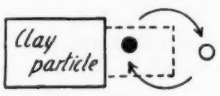

FIGURE 1

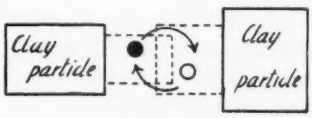

FIGURE 2

same surface and gives rise to the phenomenon of surface migration of ions. On the other hand if two separate colloidal particles approach so closely that the oscillation spaces interpenetrate, conditions for *contact exchange* between the two different particles exist as shown in figure 2. In this case the reaction as such is independent of the nature of the intermicellar liquid or soil solution. To use a picturesque expression one might say that the ions do not enter the soil solution *per se* but, in the moment of contact, jump directly from one particle to another.

The above considerations refer to ion transfer between particles of equal sign of any colloidal system. If roots with negative surfaces are immersed in colloidal clay suspensions (negative particles) there is good reason to believe that contact exchange might enter into play. Nutrient cations adsorbed on clay particles could thus become attached to plant roots directly, rather than by way of the soil solution. Since contact exchange involves a mutual transfer of ions, it follows that for every cation gained by the root an equivalent number of ions must leave the root surface and be transferred to the clay. For this reason we must distinguish between *contact intake* and *contact depletion*, as depicted in figures 3 and 4.

The experiments presented in this paper were designed to search for the

existence of contact phenomena between plant roots and colloidal clay particles. All efforts were concentrated on the phenomenon of contact depletion which is a particularly striking one, since the soil solution theories do not operate with the concept of depletion of roots. In this first paper data on the element potassium only will be reported.

Experimental Technique.—All experiments were conducted with barley plants of the Sacramento variety. They were grown according to the method of Hoagland and Broyer[2] and were used when they were three weeks old and about 18 inches high. The following types of systems were investigated.

(a) *Excised Roots.* About 100 grams of fresh roots were immersed in three liters of solution and aerated to insure optimum conditions for metabolism (Hoagland and Broyer[2]).

(b) *Decapitated Plants.* The shoots were cut off $^3/_4$ inches above the seed hull. Only the roots were dipped into the solution which was contained in shallow Pyrex trays.

(c) *Entire Plants.* The plants were left undisturbed, and roots and shoot were analyzed separately.

In all experiments listed under (a), (b) and (c) the roots were left in the solutions for a period of 10 hours. The loss of K was ascertained by analysis of the plant material using the cobaltinitrite method.[3]

(d) *Experiments with Radioactive Potassium.* The root systems of entire plants were kept for a few hours in KNO_3 solutions containing radioactive K. As soon as the shoot had accumulated substantial amounts of the radioactive element, the plants were transferred to the desired solutions. The outgo of K was determined by radioactive analysis of the solutions (Geiger counter).

Behavior of Roots in Distilled Water.—At the outset it was necessary to determine the loss of K when roots were placed in distilled water. For excised roots the data given in the table below are representative. The K content of the root is expressed as milliequivalents of K per 100 g. of dry roots. In all cases the losses are small and within experimental error. Special attention should be called to the last two rows of the table giving data for roots continuously leached for 10 hours with distilled water at a rate of ten gallons per hour. Nevertheless, the roots maintained their potassium level.

DRY WEIGHT OF ROOTS (168 PLANTS)	K CONTENT OF ROOTS M. E./100 G.	DIFFERENCE, PER CENT	REMARKS
3.66	43.1	...	Untreated
3.76	42.5	−1.4	In 3 liters H_2O
3.81	42.3	−1.9	In 3 liters H_2O
3.99	42.2	−2.1	In 100 gallons H_2O
3.55	41.4	−4.0	In 100 gallons H_2O

Similar tendencies were observed for plants which were allowed to accumulate radioactive K and then were kept in distilled water (7 plants in 400 cc.) for 4–7 hours. The radioactivity of 25 cc. of water corrected for background and radioactive decay and expressed in terms of "counts per minute" recorded by the Geiger counter is as follows:

$$H_2O \text{ (3.72 hour period)} = 8.1 \pm 3.82$$
$$H_2O \text{ (6.53 hour period)} = 6.6 \pm 5.36$$

The loss of radioactive K is small, less than 0.17 per cent and is statistically not significant. Evidently the low salt roots under investigation have a pronounced capacity to retain potassium against distilled water.

Behavior of Roots in Salt Solutions.—Since clays carry adsorbed cations, particularly Na, NH_4, Ca or Mg, the question naturally arises whether these ions *per se* exert some specific influence on the condition of the root in relation to its power of retention of potassium. Accordingly, excised roots were kept for 10 hours in three liters of the following solutions containing 3–5 milliequivalents per liter: NaCl, $NaHCO_3$, NH_4HCO_3, $CaCl_2$ and $MgCl_2$. In all cases the loss of K was small and did not exceed 4 per cent, which is still within experimental error. A HCl solution which was maintained at pH = 4.1 lowered the K content of the root by 5.1 per cent, a value which probably is significant.

A different picture is revealed by the more sensitive radioactive technique applied to entire plants. Their roots were kept for 11 hours in 900 cc. of various electrolyte solutions containing 5 milliequivalents of cations per liter and, in each case, 0.5 milliequivalents $CaCl_2$. The following counts above background were obtained on 25 cc. of solution (background = 19.8 ± 1.62):

H_2O	=	8.9 ± 7.00	KCl	=	42.8 ± 9.78
LiCl	=	−6.9 ± 7.22[4]	KNO_3	=	47.2 ± 9.50
NaCl	=	−11.5 ± 7.34	K_2SO_4	=	40.4 ± 9.78
KCl	=	62.5 ± 10.5	KH_2PO_4	=	47.1 ± 10.80
NH_4Cl	=	188.8 ± 17.7	$KHCO_3$	=	35.7 ± 10.67
HCl	=	219.4 ± 11.75			

A lyotropic series of monovalent cations for the removal of radioactive K from roots is indicated. The values for H_2O, LiCl and NaCl fall within the variability of the background (cosmic rays) and are not significant. In the cases of NH_4Cl and HCl the relatively high K outgo may have been in part a consequence of injurious effects of high electrolyte concentrations. A corresponding set with K salts (3.0 milliequivalents per liter) showed that inorganic anions which are common to nutrient solutions exerted no specific influence. The counts from systems containing $MgCl_2$, $CaCl_2$, $SrCl_2$ or $BaCl_2$ did not exceed the background. Regarding the actual

amounts of K involved, no definite figure can be given, except that the minimum amount of K lost by the roots is 0.000213 milliequivalents per 25 cc. per 100 counts.

Behavior of Roots in Colloidal Clay Suspensions.—The suspensions used in this study were of bentonite clay and of Yolo clay, both consisting of the common clay mineral montmorillonite. The bentonites were electrodialyzed and then converted into the desired basic clays by addition of hydroxides, according to the equation H-clay + NaOH = Na − clay + HOH. The Yolo clays were subjected to leaching with neutral salts. The cation adsorption capacity (base exchange capacity) was 100 milliequivalents per 100 g. for the bentonites and 55 milliequivalents per 100 g. for the Yolo colloids as determined by the ammonium acetate method.

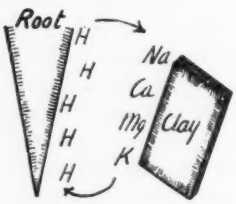

FIGURE 3

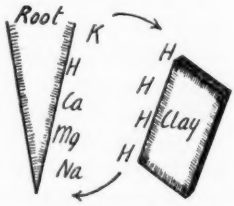

FIGURE 4

If excised roots are immersed in H or Ca-H bentonite suspensions for ten hours they suffer heavy loses of K as seen from the following data:

SYSTEM	CLAY CONCENTRATION, PER CENT	INITIAL pH OF SUSPENSION	K IN ROOTS M. E./100 G.	DIFFERENCE DUE TO COLLOID, PER CENT
H_2O	..	..	45.9	....
H-bentonite sol	3.97	3.05	4.7	−89.8
H-bentonite flakes	5.17	3.70	34.3	−26.0
K-H-bentonite sol	0.83	4.90	59.0	+28.5
Ca-H-bentonite sol	0.48	5.65	37.0	−19.4

The roots which lost 90 per cent of their total potassium showed indications of injury. From K-H-bentonite the roots accumulate K but lose Ca to the extent of 22.2 per cent. From Ca-H-clay they take up Ca ions (6.4 per cent) but lose K. The intake and outgo of nutrient ions is, therefore, of a differential nature. Coarse suspensions (flakes) are less effective than highly dispersed sols, as would be expected if contact phenomena are involved.

Furthermore, if excised roots are separated from H-bentonite suspensions (pH = 3.58) by a membrane which permits easy passage to ions but bars colloidal particles from contact with roots, no losses of K occur.

Likewise, if excised roots are suspended in a positive iron hydroxide sol (0.33 per cent) the lowering of the K level of the roots amounts to only 4.4 per cent. This is in harmony with the contact exchange theory according to which the negative barley roots[5] should not transfer cations to positive colloids.

Experiments with plants which were decapitated $^3/_4$ inches above the base of the shoot fully corroborate the results obtained with excised roots, as shown in the following table:

SYSTEM	CLAY CONCENTRATION, PER CENT	INITIAL pH OF SUSPENSION	REDUCTION OF K CONTENT OF ROOTS, PER CENT
H-bentonite	0.53	3.85	26.8
Na-bentonite	0.48	7.35	14.8
NH_4-bentonite	0.41	7.25	32.6
Ca-bentonite	0.31	7.40	0.9

It appears that the nature of the adsorbed cation, rather than the pH of the suspension regulates the magnitudes of the K extraction by the colloidal particles; Ca-clay, in the concentrations used, did not influence the K status of the root systems.

Turning to radioactive experiments, the clay sols were compared with salt solutions, both systems containing equal amounts of cations. For 7 plants in 900 cc. liquid (5.0 milliequivalents cation + 0.5 milliequivalents $CaCl_2$ per liter) the following counts above background were obtained from 25 cc. solution after a contact period of 53 hours:

$H_2O = 7.1 \pm 6.45$

$NaCl = 4.2 \pm 6.41$	$NH_4Cl = 668 \pm 49.8$
Na-Yolo colloid $= 606 \pm 92.5$	NH_4-Yolo colloid $= 1044 \pm 62.2$

Again the colloidal solutions are more effective than the true solutions, particularly in the case of the Na systems. With an improved technique of counting, the following measurements were made on divalent systems (2.2 milliequivalents cations per liter) which had 7 plants in 400 cc. solution for a period of 3.7 hours (counts above background, on 25 cc. solution):

$H_2O = 8.1 \pm 3.82$	$CaCl_2 = 11.3 \pm 3.68$
$MgCl_2 = 3.3 \pm 4.06$	$CaCO_3 = 17.0 \pm 3.50$
Mg-Yolo colloid $= 109 \pm 6.44$	Ca-Yolo colloid $= 66.3 \pm 3.81$

The greater efficiency of the clay systems as compared with the chloride salt solutions for extracting radioactive K from the roots is beyond doubt.

The influence of salt concentration and clay concentration on the removal of radioactive K from roots is illustrated in figure 5. The comparisons include KCl, $CaCl_2$, K-Yolo and Ca-Yolo colloids. Two features are outstanding. First, the effects of monovalent cations exceed those of the divalent cations; second, the clay systems uniformly give higher counts

than the salt solutions. These data convincingly prove the importance of root-colloid effects. The results obtained with the radioactive technique fully substantiate the observations made with excised roots and decapitated plants.

Injury Tests.—The root systems of entire plants were immersed in H-bentonite sols (0.16 per cent) until they had lost 20.0 per cent of their total potassium. When these roots were transferred to nutrient solutions and

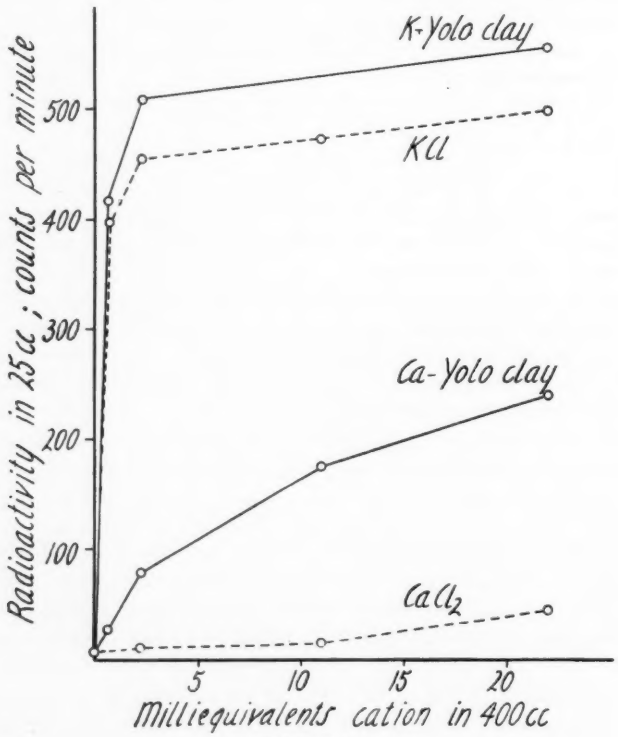

FIGURE 5

kept there for 12 hours they accumulated K to the extent of 153 per cent of their original K content. Apparently the clay treatment had not impaired the capacity for salt accumulation; in fact, the roots which had been in the bentonite sol proved to be just as efficient absorbers as the control roots which were not in contact with the clay.

A set of radioactive K roots (84 plants) were kept in a K-Ca-clay suspension for six hours, and during this time they continuously lost large

amounts of radioactive K. When these plants were transferred to distilled water the outgo of radioactive K immediately fell to such small magnitudes that the counts of the water did not exceed those of the background. It must be concluded that if any root injury occurs it can hardly be attributed to contact as such; rather it must be considered a consequence of resulting disturbances of the electrolyte balance within the plant system.

New Aspects of Plant Nutrition.—The barley plants grown by the technique referred to in this article possess an inherent capacity for pronounced accumulation of various nutrient cations. The radioactive tests reveal that during intake there occurs, simultaneously, a release of nutrient cations to the surrounding medium.

Particularly striking are the observations with radioactive K roots immersed in KCl or K-clay (figure 5). Potassium from the nutrient medium moves into the plant whereas K contained in the root is migrating out. In the case of 10 per cent K-clay (figure 5) the roots transferred about 10 per cent of their radioactivity to the clay particles.

Quantitative insight is gained from the following crucial experiment. Eighty-four radioactive plants were placed for 5 hours in a K-Ca-bentonite suspension (0.35 per cent). The roots weighed 4.51 g. (oven dry) and contained initially 1.685 milliequivalents K. At the end of the experiment they contained 2.840 milliequivalents K, a gain of 1.155 milliequivalents or 68.3 per cent. This latter value represents only the net intake. Actually the roots must have absorbed larger amounts of K because they simultaneously yielded at least 0.114 milliequivalents K to the clay, as indicated by the outgo of radioactive potassium.

In view of these findings, our concepts of the mechanism of mineral absorption by plants must be modified and extended. The results show that the intake of ions is not an uni-directional process; ions of the same species may move into the root and out of the root at the same time. The outgo is especially pronounced when the roots are in contact with colloidal systems. Accumulation and depletion are only net effects of ionic movements.

Acknowledgments.—The authors are indebted to Professor D. R. Hoagland for his interest and valuable suggestions, to Professor E. O. Lawrence, Director of the Radiation Laboratory, for supplying radioactive potassium and to Mr. A. D. Ayers for technical assistance.

A detailed account of the experiments will be published in Soil Science.

[1] Jenny, H., *Jour. Phys. Chem.*, **40**, 501 (1936).

[2] Hoagland, D. R., and Broyer, T. C., *Plant Physiol.*, **11**, 471 (1936).

[3] Hibbard, P. L., and Stout, P. R., *Jour. Assoc. Offic. Agric. Chem.*, **26**, No. 1, 137 (1933).

[4] This negative value was obtained as follows: Ten readings of the background gave

a value of 19.8 ± 1.62. Ten readings of 25 cc. of LiCl solution gave a count of 17.7 ± 1.62 which is within the variability of the background. The difference, −2.2 ± 2.29 multiplied by the radioactive decay factor of 3.15 gives the tabulated value, −6.9 ± 7.22.

[5] That the roots are negative is indicated by measurements of streaming potentials, and moreover by the fact that positive particles of iron hydroxide strongly adhere to the root while negative clay particles do not show such a behavior. The dried, ground roots have a cation adsorption capacity of about 11 milliequivalents per 100 g. as determined by the ammonium acetate method.

ON LOCALLY CONNECTED SETS AND RETRACTS

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In the present Note we propose to summarize a few results on locally connected sets and retracts. For the definitions we refer the reader to an earlier paper.[1] By way of notation we designate here by LC^*, LC^{**} the types designated by LC, $\overline{LC}$, loc. cit. Likewise instead of *semi-singular* complex, we shall say *partial realization* of a complex. The comparison with the retracts (loc. cit., Theorem II) reads now: $LC^* = ANR$, $LC^{**} = AR$.

A closed locally finite (with finite stars) simplicial geometric complex $\mathfrak{K}$ with countable elements $\sigma^1, \sigma^2, \ldots$ is said to be *regular* whenever diam. $\sigma^i \longrightarrow 0$ with $1/i$. Similarly a partial or full realization L of $\mathfrak{K}$ on a metric space $\mathfrak{R}$ is *regular* whenever if ζ^i is the sum of the faces of σ^i already realized, diam. $\zeta^i \longrightarrow 0$ with $1/i$. A continuous complex K which is the extension of L to $\mathfrak{K}$ minus a finite closed sub-complex is said to be an *almost* full realization of $\mathfrak{K}$.

In the sequel $\mathfrak{R}$ shall designate a compact metric space.

THEOREM 1. *N. a. s. c. for* $\mathfrak{R}$ *to be* LC^p *is that every regular partial realization of a complex such as* $\mathfrak{K}$, *where dim* $\mathfrak{K} \leq p$, *may almost be extended to a full realization* K *of* $\mathfrak{K}$. *For* LC^* *the result is the same without dimensional restriction, and likewise for* LC^{**} *except that* K *must be a full realization.*

If we compare with Theorem I of our paper and the LC^*, LC^{**} definitions, we find that the ϵ, η conditions are replaced by the "structure" of the infinite complexes.

Let now $\mathfrak{K}$ be a finite simplicial geometric complex and let U map $\mathfrak{K}$ on $\mathfrak{R}$, thus giving rise to a continuous complex K on the latter. We assign to K the dimension of $\mathfrak{K}$. Let now A be a set on $\mathfrak{R}$ and let it be mapped by W on the set A' of the same space. If there exists a mapping V: $A \longrightarrow \mathfrak{K}$

such that $W = UV$, A is said to be *transformed* onto K on $\mathfrak{R}$. If W is a deformation A is said to be *deformed* onto K over $\mathfrak{R}$ (ϵ *deformed* when W is an ϵ deformation). These definitions are readily shown to depend solely upon K and not upon the particular antecedent $\mathfrak{R}$ of K chosen.

THEOREM 2. *When* $\mathfrak{R}$ *is* LC^p, *every closed subset of* $\mathfrak{R}$ *whose dimension* $q \leq p$, *may be* ϵ *deformed whatever* ϵ *into a continuous complex whose dimension* $\leq q$.

THEOREM 3. *N. a. s. c. for* $\mathfrak{R}$ *to be* LC^* *is that the space be* ϵ *deformable whatever* ϵ *into a finite continuous complex. The N. a. s. c. for* LC^{**} *are the condition just stated plus contractibility.*

The last two theorems bear considerable analogy with the "polytope" theorems of Alexandroff. We may also extend Theorem III of our paper, and many similar results, by the substitution of an LC^{**} space for the Hilbert parallelotope. Finally the same theorems, suitably reworded if need be, in terms of chain-deformation, may be extended to the *HLC* class.[2]

[1] S. Lefschetz, *Ann. Math.*, **35**, 118–129 (1934). The LC^* spaces are those for which the extension of Theorem I of the paper may be carried out with a fixed $\eta(\epsilon)$, independent of p. The LC^{**} spaces are those in which in addition the extension may always be carried out without regard to the meshes of the complexes. That is to say any partial realization may be extended to a full realization.

[2] For the relation between the *LC* and *HLC* classes, see S. Lefschetz, *Duke Jour.*, **1**, 1–19 (1935); **2**, 435–442 (1936).

CONFORMAL GEOMETRY OF HORN ANGLES OF SECOND ORDER

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I. *Introduction.*—In preceding papers,[1] a study of the conformal geometry in a plane of horn angles of first order was made. In this paper, we wish to develop the conformal geometry of horn angles of second order. In the earlier papers, a fundamental differential conformal invariant of the third order was found for a horn angle of first order. In our new work, we shall study a fundamental conformal invariant of the fifth order for a horn angle of second order.

The total geometry of horn angles is non-archimedian: for each order of horn angle we have to introduce a new special Finsler metric, the appropriate Finsler space increasing in dimensionality and having a more complicated distance element as the order increases.

A *horn angle of second order* consists of an ordered pair of curves which pass through a given point in a common direction and which possess the same curvature but distinct rates of variation of curvature at the given point. Thus the curves of a horn angle of second order have three (but *not* four) consecutive points in common at the given point. In our previous work,[2] it was shown that *a horn angle of second order possesses a unique absolute conformal invariant* M_{12} *of the fifth order* (*which depends only on the first five derivatives of the two curved sides of the horn angle at the given point*). By this, it is meant that two given horn angles of the second order can be transformed into one another by a *formal* conformal transformation if and only if the two horn angles have the same M_{12} (and the sign of $\gamma_2^{1'} - \gamma_1^{1'}$ is the same for both horn angles). From this theorem, we see that, in order to study the conformal geometry of horn angles of second order, it is necessary merely to study the conformal geometry of differentiable elements of the fifth order which pass through a given point in a given direction and which have the same curvature.

A *differential element of the fifth order* is, of course, defined by a point and the first five successive derivatives at that point, that is, by a set of seven numbers. In the remainder of this paper, whenever we speak of a *curve*, we shall mean a differentiable element of the fifth order. By a *horn set* (γ), we shall mean the totality of all curves (fifth order elements) which pass through a given point in a common direction and which possess the same curvature γ. Let x be the first derivative of the curvature γ with respect to the arc length $\left(\text{that is, } x = \frac{d\gamma}{ds}\right)$ of any curve C of the horn-set (γ), y the second derivative of the curvature γ $\left(\text{that is, } y = \frac{dx}{ds} = \frac{d^2\gamma}{ds^2}\right)$ and z the third derivative of the curvature γ $\left(\text{that is, } z = \frac{dy}{ds} = \frac{d^2x}{ds^2} = \frac{d^3\gamma}{ds^3}\right)$. Then any curve C of a horn-set (γ) may be defined by the three numbers (x, y, z). Thus we can think of a horn-set (γ) as being a three dimensional space K_3 where any point of K_3 is a curve C of the horn-set (γ).

We shall call any arbitrary set of ∞^1 curves of a horn-set (γ) a *series of the horn-set* (γ). Thus any series of a horn-set (γ) is given by the two equations $y = y(x)$, $z = z(x)$, where y and z are arbitrary functions of x. A special type of series is the linear series. By a *linear series*, we mean any series whose equations are $y = px + r$, $z = qx + s$, where p, q, r, s are constants. Thus a linear series consists of ∞^1 curves of a horn-set (γ) whose first derivative $x = \frac{d\gamma}{ds}$, second derivative $y = \frac{d^2\gamma}{ds^2}$ and third deriva-

tive $z = \frac{d^3\gamma}{ds^3}$ of the curvature γ with respect to the arc length satisfy two linear equations.

We term an arbitrary set of ∞^2 curves of a horn-set (γ) a *congruence of the horn-set* (γ). Thus any congruence of the horn-set (γ) is given by the single equation $z = z(x, y)$, where z is an arbitrary function of x and y. A special kind of congruence is the flat congruence. By a *flat congruence*, we mean any congruence whose equation is $z = ax + by + c$, where a, b, c are constants. Thus a flat congruence consists of ∞^2 curves of a horn-set (γ) whose first derivative $x = \frac{d\gamma}{ds}$, second derivative $y = \frac{d^2\gamma}{ds^2}$ and third derivative $z = \frac{d^3\gamma}{ds^3}$ of the curvature γ with respect to the arc length satisfy a single linear equation.

It is found that the group of conformal transformations induces a *fundamental five-parameter group* G_5 between the curves of a horn-set (γ) and the curves of a second horn-set (Γ). It is our purpose to study the geometry of this fundamental group G_5. Under G_5, linear series are transformed into linear series and flat congruences are converted into flat congruences. It is found that *a horn-set* (γ) *is an affine three-space* K_3. In this paper, we shall obtain the elementary conformal invariants of the curves, linear series and flat congruences of a horn-set (γ).

II. *The Fundamental Group* G_5.—Let C be any curve and let D be the transformed curve under any conformal transformation. Upon finding the first derivative $X = \frac{d\Gamma}{dS}$, the second derivative $Y = \frac{d^2\Gamma}{dS^2}$ and the third derivative $Z = \frac{d^2\Gamma}{dS^3}$ of the curvature Γ with respect to the arc length S of the transformed curve D in terms of the first derivative $x = \frac{d\gamma}{ds}$, the second derivative $y = \frac{d^2\gamma}{ds^2}$ and the third derivative $z = \frac{d^3\gamma}{ds^3}$ of the curvature γ with respect to the arc length s of the curve C, it is found after lengthy calculations (using either the method of power series, or of successive differentiation of the Cauchy-Riemann equations) that any curve $C(x, y, z)$ of the horn-set (γ) is transformed into a curve $D(X, Y, Z)$ of the horn-set (Γ), which is given by the equations

$$\begin{aligned} X &= m^2x + h, \\ Y &= m^3y + 2mnx + k, \\ Z &= m^4z + 5m^2ny + (5n^2 + \Gamma^2m^2 - \gamma^2m^4)x + l, \end{aligned} \tag{1}$$

where $m \neq 0$, h, k, l are constants. *Thus the group of conformal transformations induces a five-parameter group* G_5 *between the curves of the horn-*

set (γ) *and the curves of the horn-set* (Γ). *This is our fundamental group* G_5. From the equations (1), it is immediately obvious that *a horn-set* (γ) *is an affine three-space.*

III. *The Conformal Measure* M_{12} *of a Horn Angle of Second Order.*—THEOREM 1. *Under* G_5, *any curve of a horn-set* (γ) *can be transformed into any other curve of a horn-set* (Γ). *A horn angle of second order* (*that is, an ordered pair of curves of a horn-set* (γ)) *has the unique absolute differential conformal invariant*[3]

$$M_{12} = \frac{(x_2 - x_1)^3}{4(x_2 - x_1)(z_2 - z_1) - 5(y_2 - y_1)^2 - 4\gamma^2(x_2 - x_1)^2}; \quad (2)$$

also the sign of $x_2 - x_1$ *is invariant.*

Theorem 1 is an immediate consequence of the equations (1). A complete proof of this result is given in the paper by Kasner, "The Two Conformal Invariants of Fifth Order" (loc. cit). By means of Theorem 1, we define M_{12} as the *conformal measure* of the horn angle of second order. Thus *any horn-set* (γ) *is a special type of Finsler three-space with the special Finsler metric*[4]

$$ds = \frac{dx^3}{4dxdz - 5dy^2 - 4\gamma^2 dx^2}. \quad (3)$$

This metric is non-riemannian and therefore non-euclidean. We define the length of arc of a series $y = y(x)$, $z = z(x)$ of a horn-set (γ) as the integral

$$s = \int \frac{dx}{4z' - 5y'^2 - 4\gamma^2}. \quad (4)$$

IV. *The Null Series of a Horn-Set* (γ).—We shall call a series of a horn-set (γ) a *null series* if the conformal measure of any horn angle of the series is either zero or infinity or indeterminate. From (2) or (3), it follows immediately that the null series of a horn-set (γ) are given by the Monge differential equation

$$4z' - 5y'^2 - 4\gamma^2 = 0; \quad (5)$$

together with the exceptional linear series

$$x = \text{constant}. \quad (6)$$

V. *The General Linear Series.*—A linear series is said to be a *general linear series* if it is not tangent to a null series (that is, the general linear series and the null series cannot have two consecutive curves in common). Thus, the linear series

$$y = px + r, \quad z = qx + s, \tag{7}$$

is a general linear series if and only if

$$4q - 5p^2 - 4\gamma^2 \neq 0. \tag{8}$$

From (1), we find that *under* G_5, *any general linear series of a horn-set* (γ) *is converted into a general linear series of a horn-set* (Γ). The transformation between the linear series of the two horn-sets is given by the equations

$$\begin{aligned} P &= mp + \frac{2n}{m}, \\ Q &= m^2q + 5np + \frac{5n^2}{m^2} + \Gamma^2 - m^2\gamma^2, \\ R &= m^3r - hmp - \frac{2nh}{m} + k, \\ S &= m^4s + 5m^2nr - h(m^2q + 5np + \frac{5n}{m^2} + \Gamma^2 - \gamma^2m^2) + l. \end{aligned} \tag{9}$$

From (9), we find

THEOREM 2. *Two general linear series of two horn-sets are equivalent to one another under* G_5 *if and only if the sign of*

$$4q - 5p^2 - 4\gamma^2 \neq 0, \tag{10}$$

is the same for both linear series. Two general linear series of a given horn-set have three independent invariants

$$\frac{(p_2 - p_1)^2}{4q_2 - 5p_2^2 - 4\gamma^2}, \tag{11}$$

$$\frac{(p_2 - p_1)^2}{4q_1 - 5p_1^2 - 4\gamma^2} \tag{12}$$

$$\frac{(p_2 - p_1)(s_2 - s_1) - (q_2 - q_1)(r_2 - r_1)}{(4q_1 - 5p_1^2 - 4\gamma^2)^{5/2}}. \tag{13}$$

For two intersecting general linear series (*that is, the two series have a curve* C *in common*) *possess the two independent invariants* (11) *and* (12).

In the special case where $p_2 - p_1 = 0$, we find that the ratio (12)/(11) is the appropriate invariant. A similar remark applies to Theorems 4 and 6.

According to Theorem 2, we now define the *direct dihorn angle* α_{ij} between the ordered pair of general linear series (L_i, L_j) by the formula

$$\alpha_{ij} = \frac{(p_j - p_i)^2}{4q_j - 5p_j^2 - 4\gamma^2}. \tag{14}$$

The reverse dihorn angle α_{ji} for the ordered pair of general linear series (L_i, L_j) is defined by the formula (14) where i and j are interchanged. It is found that α_{ij} and α_{ji} are entirely independent quantities.

From equations (1) and (9), we obtain

THEOREM 3. *A point and a general linear series possess the two independent invariants*

$$\frac{y - tx - r}{(4q - 5p^2 - 4\gamma^2)^{3/2}}, \tag{15}$$

$$\frac{2(z - qx - s) - 5p(y - px - r)}{(4q - 5p^2 - 4\gamma^2)^2}. \tag{16}$$

We omit the full proofs which are rather long.

VI. *The General Flat Congruence.*—A flat congruence is termed a *general flat congruence* if it is not the osculating flat congruence of any null series (that is, the flat congruence and the null series cannot have three consecutive curves in common). Thus the flat congruence

$$z = ax + by + c, \tag{17}$$

is a general flat congruence if and only if

$$5a + b^2 - 5\gamma^2 \neq 0. \tag{18}$$

By (1), we find that *under* G_5, *any general flat congruence of a horn-set* (γ) *is converted into a general flat congruence of a horn-set* (Γ). This correspondence between the general flat congruences of two horn-sets is given by the equations

$$\begin{aligned} A &= m^2a - 2nb - \frac{5n^2}{m^2} + \Gamma^2 - m^2\gamma^2, \\ B &= mb + \frac{5n}{m}, \\ C &= m^4c + (2hn - mk)b - hm^2a + \frac{5hn^2}{m^2} - \frac{5kn}{m} - h\Gamma^2 + hm^2\gamma^2 + l. \end{aligned} \tag{19}$$

By equations (19), we find

THEOREM 4. *Two general flat congruences of two horn-sets are equivalent to one another if and only if the sign of*

$$5a + b^2 - 5\gamma^2 \neq 0, \tag{20}$$

is the same for both flat congruences. The general flat congruences possess the two independent invariants

$$\frac{(b_2 - b_1)^2}{5a_2 + b_2^2 - 5\gamma^2}, \tag{21}$$

$$\frac{(b_2 - b_1)^2}{5a_1 + b_1^2 - 5\gamma^2}. \tag{22}$$

We define the *direct dihorn angle* β_{ij} between the ordered pair of flat congruences (P_i, P_j) by the formula

$$\beta_{ij} = \frac{(b_j - b_i)^2}{5a_j + b_j^2 - 5\gamma^2}. \tag{23}$$

The *reverse dihorn angle* β_{ji} is defined by the formula (23) where we interchange i and j. It is obvious that β_{ij} and β_{ji} are entirely independent quantities.

From equations (1) and (19), we find

THEOREM 5. *A curve and a general flat congruence possess the unique invariant*

$$\frac{25(z - ax - by - c)}{(5a + b^2 - 5\gamma^2)^2}. \tag{24}$$

The formula (24) gives the extremum (minimum or maximum) conformal measure between the given curve and the curves of the general flat congruence.

From equations (9) and (19), we obtain

THEOREM 6. *A general linear series and a general flat congruence possess the two unique invariants*

$$\frac{(5p - 2b)^2}{5a + b^2 - 5\gamma^2}, \tag{25}$$

$$\frac{(5p - 2b)^2}{4q - 5p^2 - 4\gamma^2}. \tag{26}$$

VII. In a later paper, we shall study the *Trihornometry of Second Order*. This is a study of the relationships between the conformal invariants of a trihorn of second order. By a *trihorn of second order*, we mean an ordered triplet of curves (C_1, C_2, C_3) which pass through a given point in a given direction such that every two curves (C_i, C_j) have three consecutive points (but not four) in common at the given point. It is found that a trihorn of second order contact possesses nine invariants: the three conformal measures M_{12}, M_{23}, M_{31}, the three direct dihorns α_{12}, α_{23}, α_{31} and the three reverse dihorns α_{21}, α_{32}, α_{13}. These nine quantities are interdependent. We find laws analogous to the identity relation for the angles of a triangle in euclidean geometry, the law of sines and the law of cosines. *In general*

it is found that four parts of a trihorn have to be given in order to determine the remaining five parts. This is entirely different from ordinary euclidean geometry and trihornometry of first order contact,[5] where only *three* parts are necessary to determine the remaining *three* parts.

[1] Kasner and Comenetz, "Conformal Geometry of Horn Angles," *Proc. Nat. Acad. Sci.*, **22**, No. 5, 303–309 (1936); Kasner, "Fundamental Theorems of Trihornometry," *Sci.*, **85**, No. 2211, 480–482 (1937); Kasner, "Trihornometry: A New Chapter of Conformal Geometry," *Proc. Nat. Acad. Sci.*, **23**, No. 6, 337–341 (1937).

[2] Kasner, "Conformal Geometry," *Proc. Fifth Internat. Congr. Math.*, Cambridge, **2**, 81 (1912); Kasner, "The Two Conformal Invariants of Fifth Order," *Trans. Amer. Math. Soc.* (1938) and "Schwarzian Symmetry," *Annals of Math.*, 1938.

[3] This is contrasted with a horn angle of first order which possesses the unique absolute conformal invariant of the third order $\frac{(x_2 - x_1)^2}{y_2 - y_1}$ where x denotes the curvature and y denotes the rate of variation of curvature at the given point.

[4] For horn angles of first order, we obtain an associated Finsler plane with the special Finsler metric $ds = \frac{dx^2}{dy}$. See Comenetz, "Kasner's Invariant and Trihornometry," *Amer. Math. Monthly*, **45**, 81–87 (1938). This metric is probably the *simplest conceivable example of a Finsler space* which is not merely riemannian.

[5] Kasner, "Trihornometry, a New Chapter in Conformal Geometry," loc. cit.

A SKELETON LIFE TABLE

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Life tables are being used considerably in vital statistics, notably by Raymond Pearl, Louis Dublin and Alfred Lotka. The accepted method of computation of life tables is the careful actuarial method used by the United States Bureau of the Census, and the Metropolitan Life Insurance Company, but many short methods of computation have been proposed with the idea of getting more quickly and easily a good idea of the expectations and of other life table functions at various ages: such are Yule's short method involving exponentials[1] and King's abridged method.[2] However, these so-called short methods still involve long computations, and often call for preliminary smoothing of the original data, which are usually too time-consuming to permit a health officer to apply the technique to local data. The method presented here seems to give very good results with remarkably few age groups, and in addition is very simple to compute.

We start with the age specific death rates, and all the rest of the work is derived from these. Let m_x^{x+h} be the per capita death rate for the age group x to $x + h$ years. We choose arbitrarily a value l_0, the number alive at age zero in a cohort. Then we compute L_0^{0+h}, the stationary population in that group; d_0^{0+h}, the deaths in the cohort during these years; and l_{0+h} the survivors at age $0 + h$; and repeat the process throughout the table. In all intervals except the first and last we take

$$L_x^{x+h} = \frac{l_x}{\frac{1}{h} + \frac{1}{2} m_x^{x+h}}; \quad d_x^{x+h} = m_x^{x+h} L_x^{x+h}; \quad l_{x+h} = l_x - d_x^{x+h}.$$

The $\frac{1}{2}$ comes from an assumption that the deaths in an interval are spread evenly throughout the interval. Between the ages of 5 and 75 this is good enough, but in other cases it is not, and when it is not, we use

$$L_x^{x+h} = \frac{l_x}{\frac{1}{h} + (1 - c)m_x^{x+h}}$$

where c is the fraction of the interval lived by those who die within the interval. This is most often used in the age group "under 5."

If the first age group is "under 1," the same formula can be used, but populations under one are apt to be poorly reported, giving too high death rates, so a simple alternative is employed. The births are used instead of the enumerated population, which divided into the deaths under one give the infant mortality. Consequently

$$d_0^1 = l_0 \times \text{I. M. (per capita)}, \text{ and } l_1 = l_0 - d_0^1$$

so we can proceed. But we shall need L_0^1 and that is equal to $l_1 + cd_0^1$.

In the last age group, it is obvious that $d_x^\infty = l_x$, so it is clear that

$$L_x^\infty = \frac{l_x}{m_x^\infty}$$

if we assume that the population from age x on can be regarded as stationary. This enables one to fill in the table. The necessary values of c are obtained from a study of the distribution of deaths by months for under one, or by single years for under five, but once determined for a given year and general area, need not be recomputed. For example, if we want to compute a life table for a county of New York State in 1930, we can get a good estimate of c from the average age of deaths of infants or small children for the total New York State, and then apply it to our county, and it will be good enough.

With the columns l_x, L_x^{x+h}, d_x^{x+h} filled in, we form a column T_x, for the

populations above age x by summing all L_x^{x+h} from the bottom up, and then the expectation $\mathring{e}_x = T_x/l_x$.

A numerical example may make this clearer (see table 1).

TABLE 1

NEW YORK STATE, ONONDAGA COUNTY, 1929–31, DEATHS IN INSTITUTIONS REMOVED

AGE	CENSUS POPUL. 1930	AVERAGE DEATHS 1929–31	m_x^{x+h}	l_x	L_x^{x+h}	d_x^{x+h}	T_x	$\mathring{e}_x$
0–1	4,950*	279.67	0.0565†	1000	953‡	56	61,322	61.32
1–4	18,835	75.00	0.00398	944	3,744	15	60,369	63.98
5–9	26,138	42.33	0.00162	929	4,624	7	56,625	60.98
10–14	25,761	34.00	0.00132	921	4,590	6	52,000	56.45
15–19	23,557	47.67	0.00202	915	4,552	9	47,410	51.81
20–24	23,842	56.00	0.00235	906	4,503	11	42,858	47.31
25–29	22,712	64.00	0.00282	895	4,445	13	38,355	42.84
30–34	23,203	72.33	0.00312	883	4,379	14	33,910	38.42
35–44	45,593	259.00	0.00568	869	8,451	48	29,531	33.98
45–54	34,559	407.67	0.0118	821	7,753	91	21,080	25.67
55–64	23,823	594.33	0.0249	730	6,487	162	13,327	18.27
65–74	13,538	721.00	0.0533	568	4,484	239	6,840	12.05
75+	5,348	746.67	0.140	329	2,356	329	2,356	7.16
	291,859	3399.67			61,322	1000		

* Average births for 1929–31. † Infant mortality. ‡ $c = .18$

NOTE: These figures are cut down from the original computation in which more places were carried.

We started with a radix of 1000. Then $1000 \times .0565 = 56$ deaths. $1000 - 56 = 994$. To get L_0^1, we took $944 + .18 \times 56 = 953$. From here on we proceeded by the regular formula, with $L_1^4 = \frac{944}{.25 + .00199} = 3744$; $d_1^4 = 3744 \times .00398 = 15$; and $l_5 = 944 - 15 = 929$; and so on. When we got $l_{75} = 329$, we immediately wrote $d_{75}^{\infty} = 329$, and then $L_{75}^{\infty} = \frac{329}{.140} = 2356$. $T_{75} = 2356$. $T_{65} = 2356 + 4484 = 6840$. $T_{55} = 6840 + 6487 = 13{,}327$, and so on, adding from the bottom up. $\mathring{e}_0 = \frac{61{,}322}{1000} = 61.32$. $\mathring{e}_1 = \frac{60{,}369}{944} = 63.98$. The sum of the d_x^{x+h} column must equal l_0, and the sum of the L_x^{x+h} must equal T_0.

The question now arises as to how good the results are—how close do they come to the results of the detailed actuarial methods? The published life tables of the United States Census for 1910 and 1920 give the raw data from which they were computed, so we can compare our work with these tables, and also with other short methods. Because King's method is

constructed for five year intervals, and Yule feels that his is valid only for five year intervals, we shall use these small age groups first, combining into larger groups later. The published figures for 1910 are computed by single years, from which we have extracted the values comparable to ours (see table 2).

TABLE 2

PHILADELPHIA FEMALES 1910. COMPARISON OF THREE METHODS

	PUBLISHED	OUR METHOD		YULE'S METHOD			PUBLISHED	KING'S METHOD[3]	
AGE	$\mathring{e}_x$	$\mathring{e}_x$	ERROR	$\mathring{e}_x$	ERROR	AGE	$\mathring{e}_x$	$\mathring{e}_x$	ERROR
0	49.60	49.51	−0.09	49.87	0.27				
5	55.14	55.16	0.02	55.12	−0.02	7	53.75	53.75	0.00
10	51.24	51.23	−0.01	51.19	−0.05	12	49.48	49.51	0.03
15	46.83	46.84	0.01	46.79	−0.04	17	45.10	45.16	0.06
20	42.61	42.63	0.02	42.59	−0.02	22	41.03	41.08	0.05
25	38.72	38.74	0.02	38.69	−0.03	27	37.19	37.23	0.04
30	34.91	34.93	0.02	34.88	−0.03	32	33.39	33.45	0.06
35	31.15	31.18	0.03	31.13	−0.02	37	29.69	29.74	0.05
40	27.49	27.52	0.03	27.47	−0.02	42	26.02	26.08	0.06
45	23.82	23.85	0.03	23.80	−0.02	47	22.37	22.43	0.06
50	20.24	20.27	0.03	20.21	−0.03	52	18.87	18.93	0.06
55	16.89	16.93	0.04	16.87	−0.02	57	15.63	15.72	0.09
60	13.88	13.92	0.04	13.85	−0.03	62	12.79	12.86	0.07
65	11.25	11.29	0.04	11.22	−0.03	67	10.30	10.40	0.10
70	8.98	9.03	0.05	8.96	−0.02	72	8.13	8.21	0.08
75	6.93	7.03	0.10	6.90	−0.03	77	6.21	6.31	0.10
80	5.23	5.30	0.07	5.22	−0.01	82	4.64	4.74	0.10
85	3.81	3.91	0.10	3.84	0.03	87	3.32	3.43	0.11
90	2.69	2.80	0.11	2.81	0.12	92	2.34	2.29	−0.05
95	1.90	2.92	1.02	2.92	1.02	97	1.65	0.88	−0.77
100	1.32	3.00	1.68	3.00	1.68				

The marked error in the last two expectations in Yule's and our methods is accounted for by the fact that the observed m_x^{x+h}'s were biologically impossible, with $m_{100}^{\infty} < m_{95}^{99} < m_{90}^{94}$. The same error does not appear in King's method since the latter provides for rejection of these values, and extrapolation to obtain substitute values. Except for these terminal entries, our method is as good as the others, and much more rapid. (Yule's method is almost as rapid if sufficiently extensive exponential tables had been available, but logarithms had to be used.)

In Whipple's "Vital Statistics" it is shown that seven groups for adjusting death rates do as well for practical purposes as eleven groups.[4] Presumably it should be possible to compute a skeleton life table including a figure for the expectation of life at birth on fewer age groups than we have just used without losing much accuracy and thereby to gain a great deal in ease of computation. Furthermore, in many cases of interest to

the health officer it is impossible to get enumerated populations or reported deaths except in fairly broad age groups so that if a life table is to be computed directly from the available data it must be of skeleton form.

Now what does happen when we use fewer groups? There are countless types of groups possible, but we shall consider those which we think would be apt to be used because of ready availability.

First, take the 13 groups used by the United States Census in publishing populations for moderately large places. The infants are kept separate from the children 1 to 4; there are five year groups from 5 to 35, and 10 year groups from 35 to 75 and all 75 and over are lumped into a final group [see table 3*a*].

TABLE 3

PHILADELPHIA FEMALES 1910. COMPARISON OF THREE GROUPINGS

	PUBLISHED	3*a* OUR METHOD		3*b* OUR METHOD		3*c* OUR METHOD	
AGE	$\mathring{e}_x$	$\mathring{e}_x$	ERROR	$\mathring{e}_x$	ERROR	$\mathring{e}_x$	ERROR
0	49.60	49.54	−0.06	49.61	+0.01	49.58	−0.02
1	55.28	55.16	−0.12			55.20	−0.08
5	55.14	55.13	−0.01	55.29	+0.15	55.17	+0.03
10	51.24	51.20	−0.04				
15	46.83	46.81	−0.02	46.96	+0.13		
20	42.61	42.60	−0.01			42.64	+0.03
25	38.72	38.71	−0.01	38.91	+0.19		
30	34.91	34.89	−0.02				
35	31.15	31.14	−0.01				
45	23.82	23.81	−0.01	24.08	+0.26	23.91	+0.09
55	16.89	16.88	−0.01				
65	11.25	11.28	+0.03	11.54	+0.29	11.28	+0.03
75	6.93	6.93	0.00			6.93	0.00

Our method fits slightly better than with the complete five year groups[5] of table 2, no matter which of the three methods is used, suggesting that perhaps the grouping acts somewhat as a smoothing of the m_x^{x+h}s. The assumption of a stationary population over 75 is not strictly valid; it gives the exact answer here, but that occurs rarely, and is not to be expected. A number of such calculations for different populations shows that there may be considerable error.

Second, for smaller places, the census often prints populations in six age groups beginning with "under 5," then two ten year groups, two 20 year groups and finishing with 65+ (see table 3*b*). Although the errors here are noticeable, still the results are probably good enough for practical purposes.

Third, we may give another grouping, with only 7 age groups, which may be made up from the 13 used above and which seem to have a some-

what greater biological or health interest than the second grouping (see table 3*c*).

We have used the enumerated populations and the reported deaths in certain age groups without smoothing or other adjustment. It is interesting to inquire what would be the result of applying our method to the age specific death rates taken out of the published life table. How well will the life table be reproduced? In five year groups, or the 13 census groups the reproduction of the table is excellent, though not notably better than when based on raw data. When done in the 6 census groups or 7 biological groups the errors seem to be considerably greater than for the computation as made directly from reported data. For other populations (than Philadelphia Females 1910) the results are similar and lead to the same conclusions, namely:

The short method of computation based on 13 census groups or the 7 so-called biological groups seems to give an entirely adequate life table for those entries computed, and the 6 census groups used for the smaller places will still give a tolerably satisfactory skeleton life table. While without a wide experience it would be impossible to tell under what circumstances, if any, the method would prove to give seriously incorrect results, a large experience indicates that the method can be recommended to health officers as likely to give sufficiently good results for their purposes, and is so short that the calculation can be made readily enough to make the life table technique almost as simple as that of adjusting death rates.

[1] "Some Life Table Approximations," by G. Udney Yule. *Proc.* Internat. Math. Cong., held in Toronto, Aug. 11–16, 1924. Vol. II, p. 873.

[2] *Length of Life*, by Louis I. Dublin and Alfred J. Lotka, p. 312.

[3] The figures for King's method as given here were the result of applying his method to the raw data—not the smoothed data which he recommends. Following his method rigidly gives a very good fit to published data, but the method was used on raw data for comparability with the other methods, and because a health officer desiring a short method would certainly be applying it to raw data.

[4] *Vital Statistics*, by George C. Whipple, p. 297.

[5] A trial of Yule's method for the groupings of table 3 indicates that it does not give such good results as ours, besides being somewhat slower in computation. We shall therefore omit further comparisons with it.

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